Elegant-crested Tinamous *Eudromia elegans* do not synchronize head and leg movements during head-bobbing

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Head-bobbing is the fore–aft movement of the head relative to the body during terrestrial locomotion in birds. It is considered to be a behaviour that helps to stabilize images on the retina during locomotion, yet some studies have suggested biomechanical links between the movements of the head and legs. This study analysed terrestrial locomotion and head-bobbing in the Elegant-crested Tinamou *Eudromia elegans* at a range of speeds by synchronously recording high-speed video and ground reaction forces in a laboratory setting. The results indicate that the timing of head and leg movements are dissociated from one another. Nonetheless, head and neck movements do affect stance duration, ground reaction forces and body pitch and, as a result, the movement of the centre of mass in head-bobbing birds. This study does not support the hypothesis that head-bobbing is itself constrained by terrestrial locomotion. Instead, it suggests that visual cues are the primary trigger for head-bobbing in birds, and locomotion is, in turn, constrained by a need for image stabilization and depth perception.

Keywords: biomechanics, bird, locomotion, pitch.

Head-bobbing, the fore–aft movement of the head during terrestrial locomotion in some birds, is an optomotor response (Friedman 1975). However, some researchers have suggested that head-bobbing may also be linked mechanically with aspects of locomotor biodynamics. Head-bobbing has two distinct phases: a hold phase and a thrust phase (Dunlap & Mowrer 1930). During the hold phase, the head is immobile (remains fixed in space) as the body travels forward, creating an illusion of backward movement of the head. The flexibility of the neck in birds (Van Der Leeuw *et al.* 2001) allows the head to remain stable as the body moves forward. During the thrust phase, the speed of the head is greater than the speed of the body, such that the head is translated to a point in front of the body. Daanje (1951) noted that the beginning of the thrust phase often occurs with the leg touchdown, whereas the beginning of the hold phase often occurs with leg liftoff, and

suggested that head movements during walking may reflect patterns observed during jumping and hopping in birds. When jumping or hopping, a bird flexes its neck prior to the hop and extends the neck during the hop. If head-bobbing during walking is simply part of the same locomotor behavioural complex as head movements during jumping and hopping, then any visual function of head-bobbing is likely to be secondarily derived. Dagg (1977) further suggested that head movement during thrust phase of the head-bob assists with shifting the bird's centre of mass (COM) forward as each leg begins to swing forward.

Importantly, head-bobbing frequency appears to be speed-dependent, such that as the forward speed of the bird increases, the proportion of the stride spent in the hold phase decreases linearly (Davies & Green 1988). At relatively high speeds, flexion and extension of the neck occur without a 'hold phase' to stabilize the head relative to the environment. At the fastest speeds, head movement is absent and the neck is extended in a constant thrust phase.

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Evidence suggesting that head-bobbing affects locomotor mechanics was found in a study of Black-headed Gulls *Chroicocephalus ridibundus* (Fujita 2006). Differences in stride characteristics were revealed in a comparison of head-bobbing and non-head-bobbing strides, with an increase in stride length and decrease in stride frequency when Black-headed Gulls bobbed their heads during walking.

Yet other evidence suggests that head movements are not always mechanically linked to locomotor movements. Neither birds walking on treadmills nor blindfolded birds exhibit head-bobbing behaviours (Frost 1978, Necker *et al.* 2000), presumably because a streaming visual signal is suppressed. Also, head-bobbing has been observed during landing when the legs are held against the body (Green *et al.* 1994). Hence, head-bobbing birds can and do have leg movements without head-bobs, as well as head-bobs without leg movements. Indeed, head-bobbing may be induced by the need to process particular types of visual signals. The hold phase is believed to function in stabilizing an image on the retina and detecting the motion of objects in the environment (Dunlap & Mowrer 1930, Davies & Green 1988). In contrast, the thrust phase is thought to facilitate motion parallax to generate depth perception: the movement of the head during thrust causes objects closer to the bird to appear to move faster than objects farther away (Frost 1978). Moreover, the thrust phase may allow for differentiation of stationary items against a background (Davies & Green 1988), an important factor for foraging birds. For example, Black-headed Gulls head-bob while foraging, but do no head-bob when they engage in non-foraging walking (Fujita 2006). Similarly, Pacific Reef Herons *Egretta sacra* and Grey Herons *Ardea cinerea* cease head-bobbing when they are not foraging (Fujita & Kawakami 2003).

The kinematics of head-bobbing have been studied most extensively in domestic pigeons *Columba livia* (Dunlap & Mowrer 1930, Frost 1978, Davies & Green 1988, Wohlschläger *et al.* 1993, Troje & Frost 2000, Fujita 2002). Documentation of head-bobbing kinematics in other species has been limited to domestic chickens *Gallus gallus* (Dunlap & Mowrer 1930, Bangert 1960, Pratt 1982), starlings (Sturnidae; Dunlap & Mowrer 1930), African Collared Doves *Streptopelia risoria* (Friedman 1975), Little Egrets *Egretta garzetta* (Fujita 2003) and Whooping Cranes *Grus*

americana (Cronin *et al.* 2005). Although the mechanics of terrestrial locomotion have been evaluated in a variety of birds (Clark & Alexander 1975, Gatesy 1999, Abourachid & Renous 2000, Reilly 2000, Verstappen & Aerts 2000, Abourachid 2001, Hancock *et al.* 2007), only four studies integrate locomotor mechanics with data on head-bobbing. Data on both leg and head kinematics are reported for pigeons (Fujita 2002), gulls (Fujita 2006), and egrets, stilts and herons (Fujita 2003, Fujita & Kawakami 2003). Only two studies (Fujita 2002, 2003) have analysed the coordination of leg and head movements, and concluded that the beginning of the hold phase began slightly after the liftoff of a leg and the beginning of the thrust phase occurred slightly before the touchdown of a leg (Fig. 1). However, this conclusion was drawn from the mean values of the difference in timing of head and leg movements. In reality, when considering the ranges and standard deviations of kinematic variables, both studies found considerable variability in the coordination of head and leg movements, suggesting that they lacked the precise coordination that might be expected were they part of a synchronized locomotor complex.

Although coordination of head and leg movements during head-bobbing behaviours has been suggested, all studies that have directly measured head-bobbing and leg events have found considerable variation in their timing. Fujita (2002) measured the duration between head-bobbing and footfall events in pigeons, but reported the
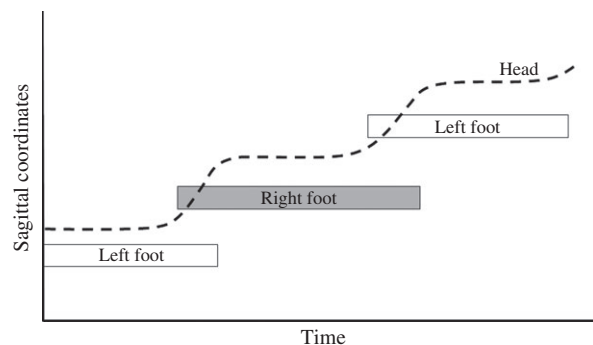

Figure 1. Fujita's (2002) proposed coordination of head (dashed line = sagittal movements (i.e. movements in the *x*-axis) of the head) and leg movements (white and grey boxes = stance phases – the beginning of each box is the time of foot touchdown and the end of each box is the time of liftoff) in a walking pigeon (modified from Fujita 2002).

durations as frames and did not calculate values relative to stance duration. Using reported values for mean, maximum and minimum durations, together with mean stance duration, an estimate of the variation in the pigeon dataset can be made: the relative duration from the beginning of hold to liftoff would range from −36 to 29% (mean = −8% ± sd = 13%) and the relative duration from the beginning of thrust to touchdown would range from −22 to 29% (17 ± 9%). Using reported values for Little Egrets (Fujita 2003), the relative intervals from the beginning of hold to liftoff would range from −5 to 37% of stride durations (8 ± 9%) and the relative intervals from the beginning of thrust to touchdown would range from −25 to 17% (−0.3 ± 9%). Although definitive assessment can only be obtained from the raw data, it appears that much variation in timing of head-bobs was documented for both pigeons and Little Egrets.

The first aim of this study was to evaluate the relationship between head-bobbing and footfall pattern over a range of speeds. Throughout the literature it is assumed that head and limb movements are synchronized during head-bobbing. However, the variation seen by Fujita (2002, 2003) suggests that the movements are not synchronized. Therefore, it is expected that the movements are coordinated but not synchronized. The second goal was to assess the effect of head-bobbing on the body's COM. It has been suggested that head-bobbing movements will shift the bird's COM forward as each leg begins to swing forward (Dagg 1977). However, Fujita (2002, 2003) found that the effect of head movements on the COM position was small. Therefore, it is expected that the movement of the head will not significantly affect the COM movement. These goals were addressed by studying the terrestrial locomotion and head-bobbing of Elegant-crested Tinamous *Eudromia elegans*.

METHODS

The dynamics of terrestrial locomotion and head-bobbing were analysed in three captive Elegant-crested Tinamous (623–865 g). This study was approved by the Institutional Animal Care and Use Committee at Ohio University (IACUC approval #U99-03). The birds were filmed in lateral view at 250 Hz using an NAC camera (Simi Valley, CA, USA) as they moved over a Kistler force platform (plate type 9281B; Amherst, NY, USA) built into a 4.9-m trackway. As the birds moved naturally along the trackway, a range of speeds was recorded. Force platform dimensions were adequate in length (0.6 m) to capture two to five steps during each trial, depending on the stride lengths of a given sequence. The force platform recorded vertical, fore–aft (longitudinal) and mediolateral (transverse) ground reaction forces (GRFs) at 1000 Hz. Video and force data were synchronized using MOTUS motion analysis software (version 7.2.6; Peak Performance Technologies, Centennial, CO, USA).

Locomotor kinematics

Reflective markers were attached to the base of the claw of the third digit, synsacrum (between the femoral heads, approximating the acetabulum) and breast (between the furcula and keel). Each marker, in addition to the left eye, was digitized in every frame within a trial using MOTUS software (version 7.2.6; Peak Performance Technologies). The mean hip height of the birds (0.17 m) was measured as the perpendicular distance from the surface of the platform to the synsacrum marker at temporal mid-stance. The forward speed of the birds was calculated videographically using the travel time of the breast marker across two 30-cm intervals marked on the back wall of the trackway and overlying the force platform. Only trials that differed in velocity by less than 10% between the initial and final intervals (steady speed) were analysed further $(100*|(v_1/v_t) - (v_2/v_t)|$, where v_1, v_2 and v_t are the forward velocity of the first half of the trial (30 cm), the second half of the trial (30 cm) and the whole trial (60 cm), respectively). Stance duration was calculated as the time from touchdown to liftoff of a given leg.

Head movements were quantified using the movement of the eye marker. The onset of the hold phase was defined as the first frame in which the x and y coordinates of the eye marker did not vary from the coordinates in the previous frame, and the onset of the thrust phase was defined as the first frame in which the x and y coordinates varied from the previous frame after a hold phase. Relative hold phase was computed as the ratio of hold duration to head-bob cycle duration (hold phase + thrust phase). A least-squares linear regression analysis was used to assess the relationship between relative hold phase and speed.

The specific timing of events was used to assess relationships between head and leg movements. Head-bobbing events were defined as the onset of hold and thrust phases, and footfall events were defined as touchdown and liftoff for both the left and the right legs. Time durations between head-bobbing events and footfall events were calculated. Specifically, the duration from liftoff to the beginning of the hold phase was calculated using the liftoff closest in time to the beginning of hold phase, regardless of whether it occurred before or after the beginning of the hold phase. Also, the duration from touchdown to the beginning of the thrust phase was calculated using the touchdown closest in time to the beginning of the thrust phase, again regardless of whether it occurred before or after the beginning of the thrust phase. Then, relative time durations were calculated by dividing time durations by the respective stance duration. First, a single-factor ANOVA was performed to determine whether the relative durations differed among individuals. As significant differences were not observed among individuals, the absolute synchronization of a head-bobbing event to a footfall event was evaluated by performing *t*-tests to determine whether the means of the relative durations equalled zero. Then, the coordination of the events was evaluated by calculating the percentage of data within 95% confidence intervals.

The pitch of the torso was approximated by torso angle, measured as the angle between the vertical axis passing through the synsacrum marker and a line passing from the breast marker to the synsacrum marker. We expect that torso pitch may be affected by two factors: locomotor movements of the body and the movements of the head and neck (Fig. 2). A moment is exerted about the pitch axis of the body when fore–aft forces cause acceleration or deceleration of the COM (Lee *et al.* 1999). The torso is expected to pitch ventrally (breast marker moves ventrally) during the braking phase of each step (from touchdown to the time of the fore–aft GRF transition), then the torso is expected to pitch dorsally (breast marker moves dorsally) during the propulsive phase (from fore–aft GRF transition to touchdown of the next leg; Fig. 2a). Therefore, a maximum torso angle is expected at each leg touchdown and a minimum torso angle at the time of fore–aft transition.

Furthermore, the need to vertically stabilize the head relative to the environment during the hold
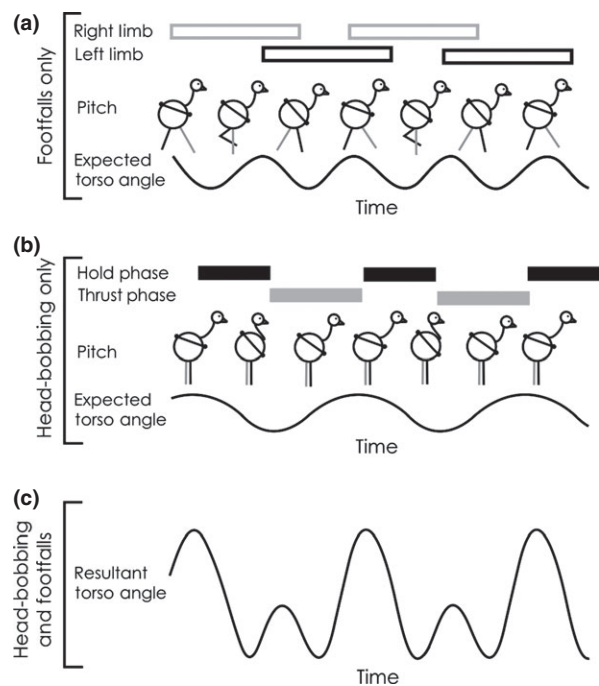

Figure 2. (a) Hypothesized effect of footfalls on torso pitch and torso angle over the time of a single trial. Open grey and black bars represent the stance phases of the right and left legs, respectively. Line drawings depict the expected torso pitch due to accelerative and decelerative forces generated by the legs (Lee *et al.* 1999). Torso pitch is represented by the orientation of the line between the synsacrum and breast. The curve represents the torso angle expected due to the pitching of the torso. (b) Hypothesized effect of head-bobbing on torso pitch and torso angle over the time of one trial. Filled grey and black bars represent thrust and hold phases, respectively. Line drawings depict the expected torso pitch due to the movements of the head and neck presuming vertical stability of the eye during stance phase. The curve represents the expected torso angle due to movements of the head and neck. (c) Hypothesized changes in torso angle resulting from the summed influences of leg and head movements.

phase is expected to result in a downward movement of the breast (ventral pitch) as the torso proceeds forward under the stabilized head and the increasingly flexed neck. During the subsequent thrust phase, the head is free to move in both the vertical and the fore–aft directions (Cronin *et al.* 2005). As a result, the extension of the neck during the thrust phase of a head-bob may cause an upward movement of the breast that would result in dorsal pitching of the torso (Fig. 2b). Thus, head-bobs alone may lead to a maximum torso angle at the beginning of hold phase and a minimum torso angle at the beginning

of thrust phase. A synchronization of leg and head movements is expected to create a regular pattern of torso angle against time (Fig. 2c), whereas an uncoupling of these movements will create unique torso angle patterns.

Centre of mass mechanics

Movement of the COM was quantified using vertical, fore–aft and mediolateral GRFs. COM movements can be used to distinguish COM mechanics (Cavagna *et al.* 1977). During slow locomotion, kinetic and gravitational potential energies of the COM cycle are out-of-phase with one another, allowing for external mechanical energy to be recovered via pendular mechanics. Conversely, during high-speed locomotion, kinetic and gravitational potential energies cycle in phase with each other, and external mechanical energy is poorly recovered via pendular mechanics. Instead, spring-mass mechanics are employed and external mechanical energy is potentially recovered by using the muscles and tendons in the legs to store and release elastic energy during each stance duration. In the present study, COM mechanics were compared in steps with a hold phase and steps within a thrust phase.

A customized LABVIEW program (National Instruments, Austin, TX, USA) was used to calculate fluctuations in kinetic (E_k) and gravitational potential (E_p) energies of the COM from the GRFs following Cavagna *et al.* (1977) and Hancock *et al.* (2007). Vertical (minus body weight), fore–aft and mediolateral GRFs were divided by body mass to determine acceleration in each direction. Each acceleration was then integrated once to obtain velocities of the COM in the three directions, and vertical velocity was further integrated to obtain vertical displacement of the COM. Average forward speed was used as the integration constant for fore–aft velocity, whereas vertical and mediolateral integration constants were estimated as the mean values for vertical and mediolateral records. Velocities were then used to calculate E_k for each direction as $E_k = \frac{1}{2} mv^2$, where m represents the animal's mass and v its velocity. Summing vertical, fore–aft and mediolateral E_k yielded total kinetic energy ($E_{k,tot}$). Gravitational potential energy was computed as $E_p = mgh$, with h as the vertical displacement of the COM. Lastly, total external mechanical energy ($E_{m,tot}$) was computed as $E_{k,tot} + E_p$.

The phase shift between $E_{k,tot}$ and E_p was calculated by dividing the time difference between the minimum values of $E_{k,tot}$ and E_p by the duration of the stride and then multiplying that value by 360° (Cavagna *et al.* 1977). Following Ahn *et al.* (2004), birds were considered to use pendular mechanics when the phase shift was between 135° and 180°, spring-mass mechanics were inferred when the phase shift was between 0° and 45°, and mixed mechanics (a combination of pendular and spring-mass mechanics) in steps with phase shift values between 45° and 135°.

The amount of external mechanical energy recovered via pendular mechanics was calculated following Blickhan and Full (1992):

$$\%R = 100^*((\Delta E_p + \Delta E_{k,tot}) - \Delta E_{m,tot})/(\Delta E_p + \Delta E_{k,tot})$$

where ΔE_p, $\Delta E_{k,tot}$ and $\Delta E_{m,tot}$ are the sums of the positive increments of the E_p, $E_{k,tot}$ and $E_{m,tot}$ profiles, respectively.

Relative times were calculated for GRF events by dividing the duration from touchdown to the event (either peak vertical force or fore–aft force transition) by the stance duration. The effect of head-bobbing on locomotor mechanics parameters (phase shift, percentage recovery, stance duration, relative peak vertical force and fore–aft force transition durations) was evaluated by comparing steps with a hold phase and steps within a thrust phase. A single-factor ANOVA was used to explore differences between individuals for each parameter. As significant differences were not observed, each parameter was compared between hold and thrust steps using a single-factor ANOVA for all individuals together.

RESULTS

Relationship of speed and footfall to head-bobbing

We obtained 60 steady speed trials with speeds ranging from 0.4 to 1.6 m/s (1.03 ± 0.27 m/s, mean $\pm$ 1 sd). Head-bobbing patterns changed predictably with speed. For trials with a head-bob, the relative hold phase duration decreased from 0.51 to 0.06 as speed increased (regression line: $y = -0.31x + 0.59$, adjusted $R^2 = 0.708$, $P > 0.001$; Fig. 3).

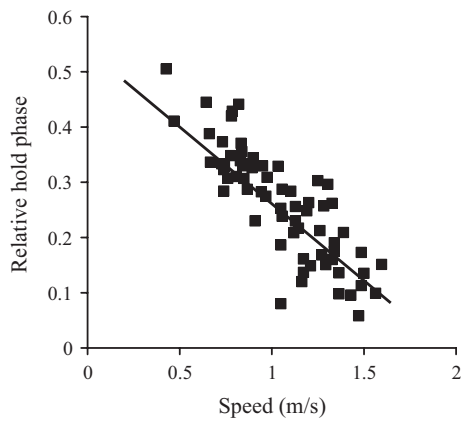One aspect of kinematics that was affected by head-bobbing was stance duration. The stance

Figure 3. Relative hold phase as a function of speed in Elegant-crested Tinamous. The solid line represents the regression line ($y = -0.31x + 0.59$, adjusted $R^2 = 0.708$, $P > 0.001$) in Tinamous.

durations of individual birds did not differ significantly. However, stance durations of steps with hold phases were significantly longer than stance durations of steps within a thrust phase ($P = 0.0009$; Fig. 4); this was especially evident at the slower speeds (< 1 m/s).

Less predictable relationships were obtained between head-bobbing and footfall events. The relative duration of time between leg touchdown and the beginning of thrust phase ranged from −0.88 to 0.53, i.e. −88 to 53% of stance duration (0.06 ± 0.29; individual birds did not differ significantly ($P = 0.1$); Fig. 5a). Although the mean
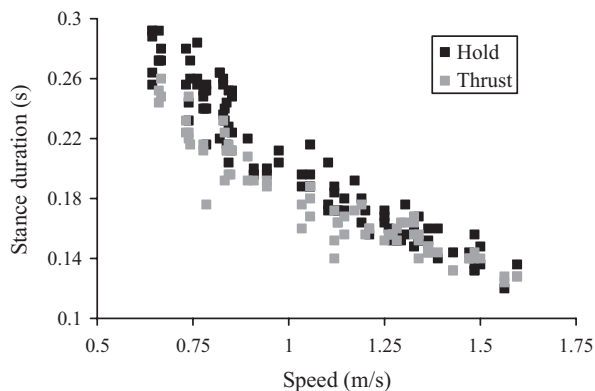

Figure 4. Stance duration as a function of speed. Black squares represent stance durations for steps in which a hold phase occurs and grey squares represent stance durations for steps entirely within a thrust phase. Stance duration is slightly longer in steps that include a hold phase ($P = 0.0009$).
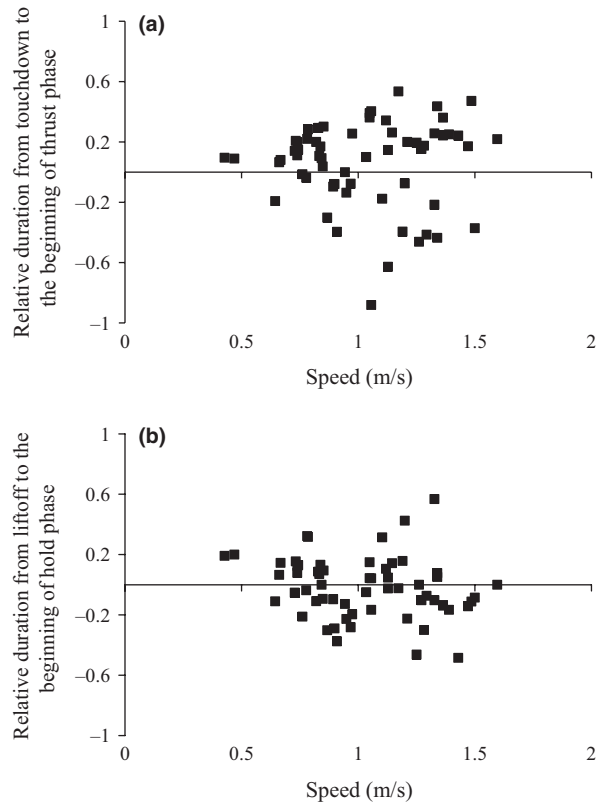

Figure 5. (a) Relative time duration between touchdown and the beginning of thrust phase as a function of speed. (b) Relative time duration between liftoff and the beginning of hold phase as a function of speed.

relative duration did not differ from zero in a *t*-test ($P = 0.1$), only 16.7% of the trials were within the 95% confidence intervals, indicating that the beginning of thrust phase and touchdown were coordinated only in this percentage of trials. The level of coordination was substantially greater in the slower trials (< 1 m/s; 31% of trials were within the 95% confidence intervals) than in the faster trials (> 1 m/s; 3% of trials were within the 95% confidence intervals). Also, the relative durations from leg liftoff to the beginning of hold phase ranged from −0.48 to 0.57, i.e. −48% to 57% of stance duration (-0.02 ± 0.20; individual birds did not differ significantly ($P = 0.1$); Fig. 5b). Again, although the mean relative duration did not differ from zero in a *t*-test ($P = 0.5$), only 13.3% of the trials were within the 95% confidence intervals, indicating that the beginning of hold phase and liftoff were coordinated only in this percentage of trials. These events were only slightly more coordinated in faster trials (> 1 m/s; 16% of trials

were within the 95% confidence intervals) than in slower trials (< 1 m/s; 10% of trials were within the 95% confidence intervals). These results show that head-bobbing movements were poorly coordinated with leg movements in a majority of the trials. This is a significant finding, suggesting that studies that only examine mean relative durations can falsely retrieve a pattern of coordinated head and leg movements, and that closer examination of the distribution of data about the mean reveals a breakdown in that pattern, such that the majority of strides do not show synchrony of head and leg movements.

Effect of head-bobbing on GRFs

GRF profiles were strongly influenced by locomotor speed, as noted by comparing fast and slow trials (top plots in Fig. 6). High-speed locomotion resulted in single-peaked vertical GRFs for each step, characteristic of animals moving with bouncing mechanics (Fig. 6a). In these fast trials, Tinamous continually extended their necks and no head-bobbing occurred. At the slowest speeds, vertical GRFs were double-peaked, typical of inverted pendular mechanics (Fig. 6d). Frequent head-bobbing
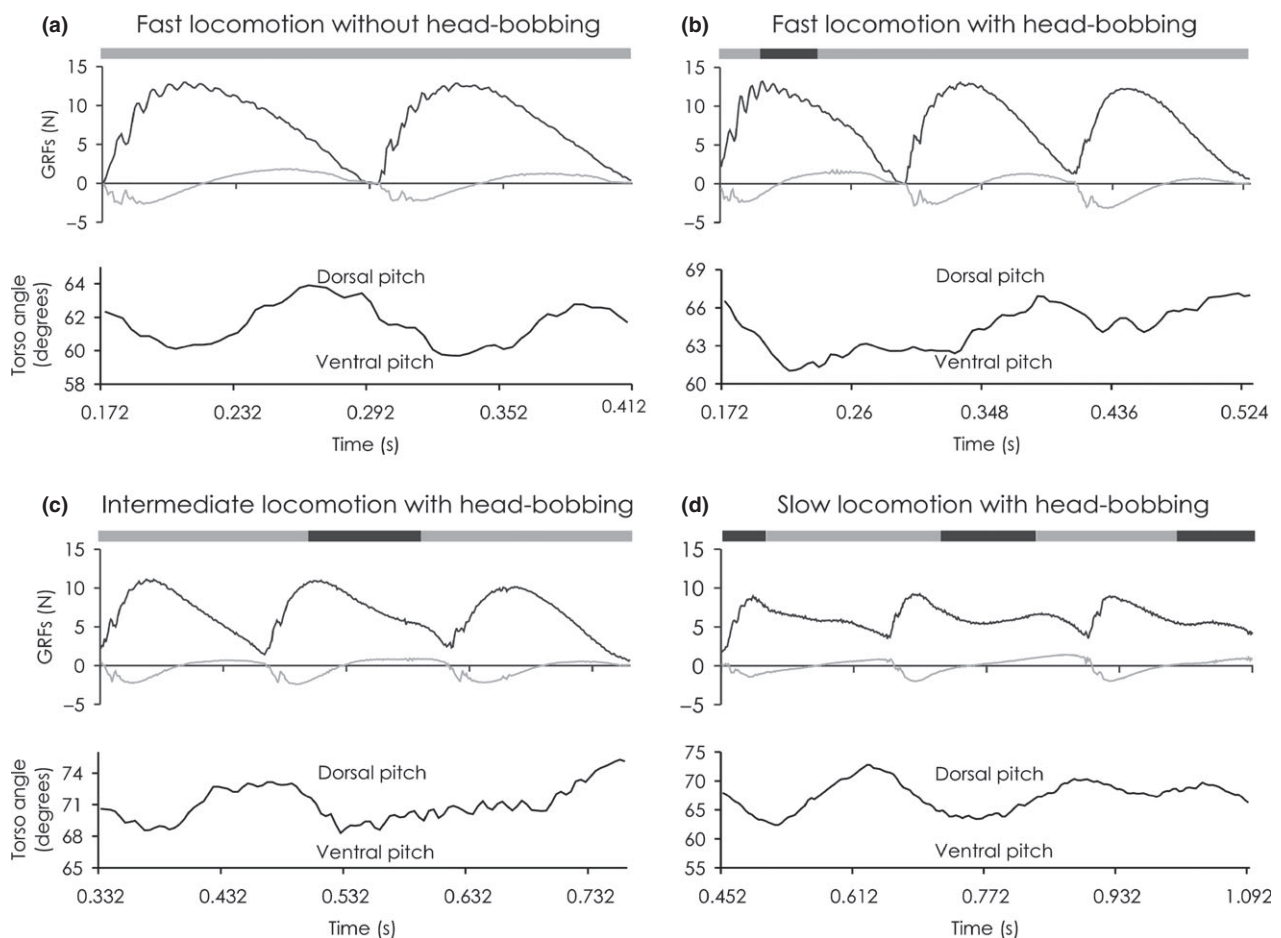

Figure 6. The top graphs in each section depict the vertical (black curve) and fore–aft (grey curve) ground reaction forces (GRFs) in four representative trials. The bottom graphs in each section show the corresponding torso angles. Grey and black bars above the graphs represent thrust phase and hold phase, respectively. (a) In a fast trial (1.74 m/s) without head-bobbing, the torso angle magnitude inversely mirrors the vertical GRFs. (b,c) In fast (1.56 m/s) and intermediate (1.13 m/s) trials with head-bobbing, the torso angle does not mirror the GRFs during the hold phase. (d) In a slow trial (0.76 m/s) with head-bobbing, hold phases occur with every step, and the correspondence between torso angle and vertical GRF depends on the timing of hold phase within an individual step (if the hold phase occurs early in a step, then the torso angle mirrors the vertical GRF; however, if the hold phase occurs at the middle or end of a step, then the torso angle does not mirror the vertical GRF).

in these trials resulted in a hold phase with every step.

Overprinted on this general pattern are modifications to the GRFs due to head-bobbing, with distinct differences in the GRFs noted between steps with a hold phase and steps within a thrust phase. This effect was most evident for intermediate speed locomotion: the vertical GRFs of steps in which a hold phase occurred were either double-peaked or plateaued (second step in Fig. 6c), whereas steps entirely within a thrust phase displayed single-peaked profiles (first and third steps in Fig. 6c). With increased speed, the effect of head-bobbing on GRF profiles was more subtle yet still evident (Fig. 6b); namely, steps including hold phases were only slightly plateaued compared with steps within a thrust phase. Thus, the vertical GRF profile differed within a single steady speed trial dependent upon whether the step exhibited a hold phase.

The timing of events in the GRF profiles was also affected by head-bobbing. The overall timing of peak vertical force relative to stance duration ranged from 0.09 to 0.40 (0.25 ± 0.07; individual birds did not significantly differ ($P = 0.9$); Fig. 7b); however, steps with a hold phase exhibited significantly earlier peak vertical force events compared with steps within a thrust phase ($P < 0.01$). Additionally, this significant difference was observed when the trials were analysed in separate speed groups ($P = 0.04$ for trials with speeds less than 1 m/s, and $P = 0.05$ for trials with speeds greater than 1 m/s). In addition, the overall timing of fore–aft force transition relative to stance duration ranged from 0.26 to 0.50 (0.37 ± 0.04; individual birds did not differ significantly ($P = 0.6$); Fig. 7a), but again steps with a hold phase exhibited an earlier fore–aft force transition than did steps within a thrust phase ($P = 0.01$). However, when the trials were analysed in separate speed groups this significant difference was only observed in trials with speeds less than 1 m/s ($P = 0.002$ vs. $P = 0.4$ in faster trials). Therefore, head-bobbing has a measurable effect on vertical GRFs at all speeds, and has an effect on fore–aft GRFs only at slower speeds.

Effect of head-bobbing on torso pitching

Both locomotor dynamics and head-bobbing affected dorso-ventral pitching of the torso. The effect of locomotor dynamics alone is best noted
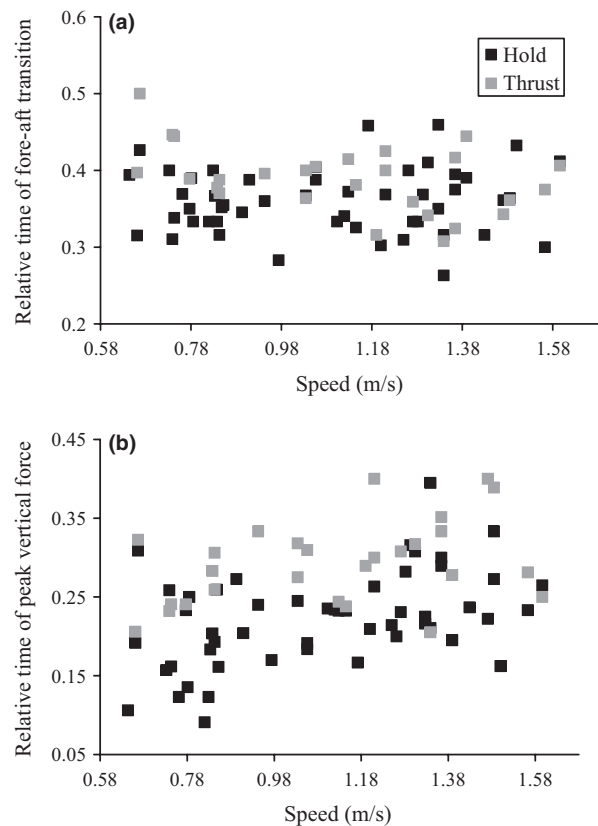

Figure 7. (a) Relative timing of fore–aft ground reaction force transition as a function of speed. Black squares represent steps in which a hold phase occurs and grey squares represent steps within a thrust phase. Steps with a hold phase exhibited significantly earlier fore–aft transitions compared with steps within a thrust phase ($P = 0.01$). (b) Relative timing of peak vertical force as a function of speed. Black squares represent steps in which a hold phase occurs and grey squares represent steps within a thrust phase. Steps with a hold phase exhibited significantly earlier peak vertical forces compared with steps within a thrust phase ($P < 0.01$).

in the fastest trials without head-bobbing (Fig. 6a). In these trials, the torso angle decreased (ventral pitch) from leg touchdown until the breaking-propulsion transition in the fore–aft force, and the torso angle increased (dorsal pitch) from the transition of the fore–aft force until the touchdown of the opposite leg. In other words, the torso pitched ventrally then dorsally during each stance phase, as hypothesized due to locomotor dynamics alone (Fig. 2a).

Locomotor dynamics continue to be the main influence on torso pitch in trials that exhibit head-bobs. However, the normal cycling pattern of the torso pitch is interrupted by the head-bob,

resulting in torso angle profiles that do not mirror the GRFs precisely. When a hold phase occurred in the second half of a fast or intermediate speed step (Fig. 6c, second step; Fig. 6b, first step), dorsal pitching of the torso caused by leg movements appeared limited by the need to accommodate neck flexion and vertical stabilization of the head. This effect is observed to a lesser degree in low-speed locomotion with head-bobbing (Fig. 6d). During the thrust phase of a head-bob, the head moves in both the horizontal and the vertical planes, and does not affect torso pitch. These data support our hypothesis that the hold phase of head-bobbing should correspond to a ventral pitching of the torso (Fig. 2). Therefore, although torso pitch and vertical GRF profiles are primarily constrained by locomotor dynamics, both are secondarily influenced by the hold phase of head-bobbing.

Effect of head-bobbing on COM mechanics

Across the entire sample, phase relationships between the minima of gravitational potential energy and kinetic energy ranged from 0° to 165.7° (Fig. 8a). Tinamous in this study predominantly engaged in bouncing mechanics (phase shift < 45° in 58% of the trials). Thirty-six per cent of trials exhibited mixed mechanics (phase shift between 45° and 135°), whereas only four trials exhibited vaulting or pendular mechanics (phase shift > 135°). No significant differences were found in phase shift between individual birds ($P = 0.1$) or between steps with a hold phase and steps within a thrust phase ($P = 0.3$). All trials with vaulting mechanics exhibited a hold phase during each step.

The amount of mechanical energy recovered using pendulum-like mechanics ranged from 0.3 to 57.6% (Fig. 8b). Trials with bouncing mechanics were associated with lower energy recoveries (range: 0–17.5%; 5.9 ± 4.1), trials with mixed mechanics tended to have intermediate energy recoveries (2.3–44.1%; 20.8 ± 12.8), and trials with vaulting mechanics exhibited high energy recoveries (33.9–57.6%; 48.1 ± 10.7). Individuals in the study sample exhibited similar energy recoveries ($P = 0.2$). Steps with a hold phase and steps within a thrust phase also exhibited similar values for energy recovery ($P = 0.3$). Therefore, COM mechanics were not demonstrably affected by head-bobbing.
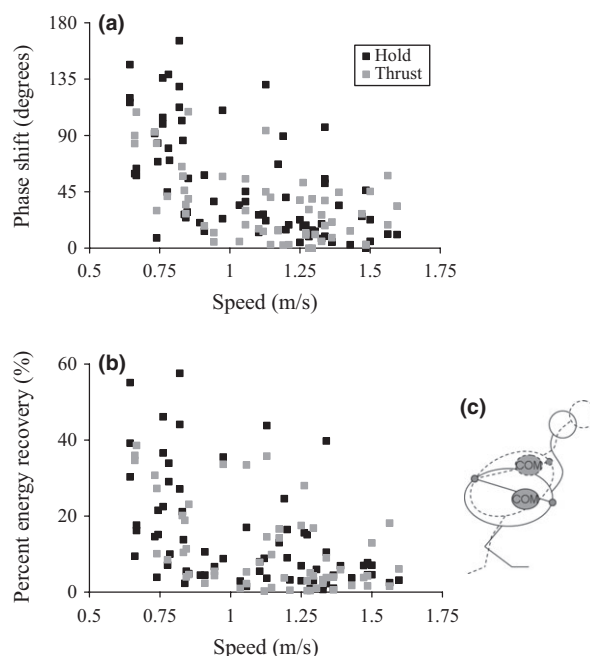

Figure 8. (a) Phase shift between the minima of E_p and $E_{k,tot}$ curves as a function of speed. Black squares represent steps in which a hold phase occurs and grey squares represent steps within a thrust phase. Phase shifts of steps with a hold phase and steps within a thrust phase are not significantly different. (b) Percentage of mechanical energy recovered via pendulum-like mechanisms as a function of speed. Black squares represent steps in which a hold phase occurs and grey squares represent steps within a thrust phase. Mechanical energy recoveries of steps with a hold phase and steps within a thrust phase are not significantly different. (c) A diagram of COM movement as a function of torso pitch. The solid line drawing represents a ventrally pitching bird during braking and the dashed line drawing represents a dorsally pitching bird during propulsion. Alterations in torso pitch result in greater vertical than horizontal displacements of the COM.

DISCUSSION

This study does not support the hypothesis that head-bobbing is itself constrained by terrestrial locomotion. Instead, it suggests that visual cues are the primary trigger for head-bobbing in birds, and that locomotion is, in turn, constrained by a need for image stabilization and depth perception.

Although the Tinamous in this study did not synchronize the timing of their head and leg movements, head-bobbing did exert an effect upon locomotion. Notably, steps with a hold phase exhibited significantly longer stance durations than did steps within a thrust phase. Also, the relative timing of peak vertical force occurred earlier in steps with a hold phase than in steps within a thrust phase. In

slower speed trials, the fore–aft transition from braking to propulsion occurred earlier in steps with a hold phase than in steps within a thrust phase; however, in faster speed trials, the fore–aft transition occurred at similar times in steps with a hold phase and steps within a thrust phase. This suggests an elongation of the steps with a hold phase, and at slower speeds, the elongation occurs during the propulsive phase. Thus, the hold phase of head-bobbing can elongate the single support phase of a stride, potentially limiting the jarring effect of the subsequent touchdown during head stabilization. As torso pitching occurs at the hip joint, ventral pitching that occurs during a hold phase acts to flex the hip joint, in turn allowing greater hip extension during propulsion. In contrast, dorsal pitching during thrust phase acts to extend the hip joint and limits hip extension during propulsion. A similar coordination of torso pitching with head-bobbing was demonstrated recently for Common Quail *Coturnix coturnix* (Abourachid *et al.* 2011).

Despite the irregularity of head-bobs relative to footfall events, head-bobbing in Tinamous does have a predictable effect on mechanics of the body's COM. The influence of the head alone on the COM is likely to be trivial, as the head and neck constitute only 5.4% of total body mass (Hancock 2010). Rather, the COM is likely to be influenced much more by compensatory torso pitching that accompanies head-bobs (Fig. 6c). The torso must pitch ventrally during the hold phase so that the head is held stable both horizontally and vertically. Rotation of the torso during pitching occurs about the hip joint. Because the Tinamou torso is largely horizontal in orientation, pitching displaces the body's COM more vertically than horizontally (Fig. 8c). Consequently, the hold phase has a greater effect on the vertical ground reaction force record than on the fore–aft force record (as seen in Fig. 6b,c). Although a difference in the timing of peak vertical force and the fore–aft transition is observed between steps with a hold phase and steps within a thrust phase (Fig. 7b), this timing of force variables does not translate into significant differences in COM mechanics or mechanical energy recovery (Fig. 8).

Although significant differences between steps with a hold phase and steps within a thrust phase were not observed in phase shift or mechanical energy recovery in this study, there is potential for the head-bobbing behaviour to affect the cost of locomotion. One way to determine this would be to compare the cost of walking with and without head-bobbing in the same birds. This could be done by comparing ground walking with head-bobbing to walking on a treadmill without head-bobbing at similar speeds. If it is found that head-bob walking is more energetically costly, then it could be concluded that the visual benefits outweigh the locomotor costs.

In conclusion, Tinamous do not coordinate head-bobbing and leg movements precisely. Yet head-bobbing does influence locomotion: steps with a hold phase have longer stance durations as well as earlier peak vertical forces and fore–aft transitions. Compensatory torso pitching to stabilize the head during hold phase has a predictable, but potentially trivial, effect on whole body ground reaction forces and mechanics. Future studies of head-bobbing and locomotor mechanics focused on birds with proportionally larger head/neck mass will reveal whether COM mechanics can be influenced by head movements in other taxa.

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